

LATE TERTIARY SEALS OF THE SOUTH ATLANTIC OCEAN

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(With 15 figures and 2 tables)

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ABSTRACT

A lectotype is designated for *Prionodelphis rovereti* Frenguelli, 1922 from Argentina and it is assigned to the Cetacea, while the monachine seal '*Prionodelphis capensis* Hendey & Repenning, 1972, from South Africa is assigned to the new genus, *Homiphoca*. A nearly complete skull and mandible is designated as a paratype of *H. capensis* and this, and other, additional material is described. *H. capensis* is morphologically intermediate between living monk seals of the genus *Monachus* (Phocidae, Monachinae, Monachini) and the seals of Antarctica (Phocidae, Monachinae, Lobodontini). It is here assigned to the latter group and, contrary to earlier opinion, is suggested to be more closely related to the crabeater, *Lobodon carcinophagus*, than any other living seal.

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INTRODUCTION

The true seals (family Phocidae), which are today widely distributed in the oceans of the world, have a very poor fossil record, and there are many uncertainties concerning their origin, evolution and dispersal (Ray 1976a).

Living Phocidae are generally divided into two subfamilies, the Phocinae and the Monachinae. The Phocinae are a diverse group comprised of the seals of northern middle and high latitudes. They include such species as the common or harbour seal (*Phoca vitulina*), the ringed seal (*Pusa hispida*) and the grey seal (*Halichoerus grypus*). The Monachinae are the subfamily to which the fossil seals discussed in this paper belong, and they are here divided into three groups. The first is the Monachini, which includes the monk seals of the Mediterranean (*Monachus monachus*), the Caribbean (*M. tropicalis*), and

Hawaii (*M. schauinslandi*) (King 1956). The second group is the Lobodontini, which comprises the seals of Antarctica, namely, the crabeater (*Lobodon carcinophagus*), leopard (*Hydrurga leptonyx*), Weddell (*Leptonychotes weddelli*), and Ross seals (*Ommatophoca rossi*) (Scheffer 1958). Thirdly, there are the elephant seals (*Mirounga leonina*, *M. angustirostris*), whose relationships to other monachines are discussed elsewhere (De Muizon 1979).

The most significant fossil Phocidae are from Miocene/Pliocene deposits in five widely separated regions. Important material has been found in the Paratethyan region, which extends from Austria to the southern Soviet Union. It has been discussed by several authors since first described by Eichwald (1853), and Grigorescu (1976) has commenced a much-needed revision. Secondly, the Antwerp Basin in Belgium has yielded a diverse assemblage of skeletal elements described by Van Beneden (1877). This material was recently revised by Ray (1976a, in press), and has also been studied by the senior author. The Calvert and Yorktown Formations in eastern North America have been the source of a wealth of material studied by Ray (1976a, in press).

The remaining two regions are in the Southern hemisphere. The Pisco Formation on the southern coast of Peru is the source of the most complete late Tertiary phocids ever discovered. This material represents five new species belonging to four new genera, and has been studied by the senior author (De Muizon 1979). The last region is the south-western coast of South Africa, with almost all the known material having come from a single locality, namely, 'E' Quarry at Langebaanweg near Cape Town. The 'E' Quarry material represents a single species, which is now the best represented fossil phocid in the world (Hendey & Repenning 1972; Hendey 1976).

Less significant material has been discovered elsewhere, including Argentina. The Argentinian material, which consists of a few isolated teeth and a mandible fragment, is identified as *Prionodelphis rovereti* (Frenguelli 1922; Cabrera 1926). It was to the genus *Prionodelphis* that the South African species (*P. capensis*) was referred.

It is the purpose of this paper to re-examine the status of the South African and Argentinian material.

SOUTH ATLANTIC LATE TERTIARY PHOCIDAE

THE ARGENTINIAN MATERIAL

Frenguelli (1922) based the identification of the new genus and species, *Prionodelphis rovereti*, from the late Miocene/early Pliocene of Argentina on two isolated teeth, one of which is obviously that of a delphinoid cetacean, while the other is a cheek tooth of a monachine seal. These two teeth are syntypes and the first illustrated specimen, the cetacean tooth (Frenguelli 1922: 492, fig. 1a), is here designated the lectotype of the species. *P. rovereti* is thus a cetacean, which is the group to which Frenguelli believed both teeth belonged, although it should

perhaps be regarded as a *nomen vanum* (Simpson 1945: 27), since a single tooth is an inadequate basis on which to identify a cetacean. The monachine tooth (Frenguelli 1922: 492, fig. 1b-c) is also of low diagnostic value and is here informally identified as *Monachinae* A.

In the second part of his paper Frenguelli (1922) assigned to *P. rovereti* three teeth which had previously been described and figured by Ameghino (1889) as those of a 'creodont', *Apera sanguinaria*. This species was identified by Ameghino (1886) on the basis of two teeth previously identified by Burmeister (1885) as 'Ferae' close to the 'felid', *Eutemnodus americanus*. These two teeth are not included amongst the three figured by Ameghino (1889) and Frenguelli (1922), which undoubtedly belong to a monachine, although not necessarily *Monachinae* A. They cannot be referred to either *Eutemnodus* or *Apera*. The latter was listed as a junior synonym of the 'creodont' *Eutemnodus* by Trouessart (1898), a view supported by Marshall (1978), although he included *Eutemnodus* in the Borhyaenidae. The three additional teeth referred to *P. rovereti* by Frenguelli (1922) are here identified as *Monachinae* B.

Cabrera (1926) realized that the *P. rovereti* hypodigm included phocid material, and noted the existence of a phocid mandible with one tooth which came from the same deposits as the two teeth described in the first part of Frenguelli's (1922) paper. Although Frenguelli (1926) doubted that *P. rovereti* was a seal, and although the matter was never clarified by the designation of a lectotype, this species became established in later literature as a phocid (e.g. Kraglievich 1934; Kellogg 1942; King 1964).

Hendey & Repenning (1972: 92) referred the far superior material from Langebaanweg, South Africa, to *Prionodelphis*, with the identification being justified by the following statements: 'In assigning the Langebaanweg phocid to the genus *Prionodelphis*, it is recognized that reassessment may be required when more material of *P. rovereti* is found. Generic identity is based upon the remarkable similarity of the few fragments from Argentina to the South African material and on the belief that the lack of greater knowledge is a stronger argument against the establishment of a new genus than it is against tentative assignment to the same genus.'

It is the three teeth of the Argentinian *Monachinae* B which are most like their counterparts in the South African species. This applies particularly to the M¹ (Frenguelli 1922: 497, fig. 2A), which resembles that of '*Prionodelphis*' *capensis* in having a strongly recurved and sharp-pointed principal cusp, although it is distinct in having a small, anterior accessory cusp closer to the apex of the principal cusp than any of the South African specimens. The two lower cheek teeth (Frenguelli 1922: 497, figs 2B-C) resemble their '*P.*' *capensis* homologues in being relatively narrow and with an inflation of the cingulum posterolingually. They are, however, distinct in having less prominent accessory cusps which are situated closer to the apices of the principal cusps.

Judging from a cast of the *Monachinae* A tooth, probably a P⁴, it differs from its counterparts in '*P.*' *capensis* by being broader, and in having the lingual

margin semicircular in occlusal view, rather than having a posterolingual expansion of the cingulum. In both these respects the Argentinian tooth is similar to the P⁴ of *Monachus monachus*. In addition, the teeth of Monachinae A and *M. monachus* are relatively high crowned, more so than those of 'P.' *capensis* and, apparently, Monachinae B.

The situation in respect of material previously assigned to *Prionodelphis rovereti* may be summarized as follows:

1. *Prionodelphis rovereti* is a cetacean, with the first figured specimen (Frenguelli 1922: 492, fig. 1a) here designated as a lectotype.
2. The second tooth figured by Frenguelli (1922: 492, fig. 1b-c) belongs to a monachine, here designated Monachinae A. It apparently represents a species closer to *Monachus monachus* than any other monachine. It is not conspecific, and may not even be congeneric with '*Prionodelphis*' *capensis*.
3. The three teeth of '*Apera sanguinaria*' described and figured by Ameghino (1889) and referred to *P. rovereti* by Frenguelli (1922: 497, fig. 2) also represent a monachine, which is here designated Monachinae B, since it is not necessarily conspecific, or even congeneric, with Monachinae A. Monachinae B is, however, close to 'P.' *capensis*, and both probably represent the same genus.

It follows that the South African seal hitherto referred to *Prionodelphis* must now be assigned to a new genus.

THE SOUTH AFRICAN SPECIES

Family Phocidae

Subfamily Monachinae

Tribe Lobodontini

Diagnosis

Monachinae characterized by the simultaneous presence of the following two features:

1. The tympanic bulla covers the petrosal posteriorly.
2. A mastoid lip overlaps the posterior wall of the bulla.

Homiphoca gen. nov.

Type species

Prionodelphis capensis Hendey & Repenning, 1972.

Amended diagnosis

A monachine phocid with a skull superficially similar to that of *Monachus*. It differs from *Monachus* in having a relatively large rostrum, which is wide posteriorly and narrow anteriorly. As in *Monachus*, but unlike Lobodontini, the premaxillae terminate against the nasals, where they are anteroposteriorly



Fig. 1. Dorsal view of *Homiphoca capensis* skull, SAM-PQ-L31976 (paratype).

elongated. The premaxillae have prominent tuberosities anteriorly. The ascending process of the maxilla is relatively high as in Lobodontini and, viewed anteriorly, is not strongly recurved medially as in *Monachus*. Dental formula: 2.1.4.1/2.1.4.1. The premolars are morphologically similar to those of *Monachus*, and unlike those of Lobodontini. They differ from those of *Monachus* in being lower crowned, relatively narrower and in having a pronounced posterolingual expansion of the cingulum. The accessory cusps on the premolars are small but distinct, while the M^1 usually lacks such cusps and is distinct in having a strongly recurved and sharp, pointed principal cusp. The M_1 is the largest of the cheek teeth, with the principal cusp slanted posteriorly, and often with a small accessory cusp low on the long anterior keel of the principal cusp. The inter-orbital region is broad and tapers posteriorly as in *Lobodon*, but unlike all other monachines. In the auditory region the tympanic bulla covers the petrosal, while the mastoid forms a lip overlapping the posterior border of the bulla.

The humerus has an entepicondylar foramen, and the tibia and fibula are fused proximally.

Etymology

From '*lhomi*' and '*phoca*', which are respectively the Hottentot and Greek words for 'seal'. The Hottentots inhabited the Langebaanweg area when Europeans first settled at the Cape of Good Hope; '*lhomi*' refers to *Arctocephalus pusillus*, a member of the family Otariidae (Budack 1977).

Homiphoca capensis (Hendey & Repenning, 1972)

Holotype

SAM-PQ-L15695—an incomplete and partly restored skull with left \underline{C} and P^4 , and right P^3 .

Paratype

SAM-PQ-L31976—an almost complete skull and mandible, partly restored, lacking right P^2 , P^4 , lower incisors, \underline{C} , P_1 and P_3 , and left lower teeth except for the lateral incisor and part of P_3 (Table 1, Figs 1-4).

Referred material

That described by Hendey & Repenning (1972) and many other specimens in the South African Museum, including:

SAM-PQ-L30080—an almost complete skull, partly restored, with parts of left P^1 to P^3

SAM-PQ-L30568—an almost complete skull and right hemimandible, partly restored, with right \underline{C} , P^1 , P^3 and M_1^1 , and left P^1 and P^3

SAM-PQ-L32101—an almost complete skull and mandible, partly restored, lacking left upper lateral incisor, P^4 and M^1 , right P_1 and P_4 , and left lower incisors, P_2 , P_4 and M_1 (Fig. 5)



Fig. 2. Lateral view of *Homiphoca capensis* skull, SAM-PQ-L31976 (paratype).

- SAM-PQ-L32415—an almost complete skull and left hemimandible, partly restored, with right upper incisors and P^2 , left P_1^1 and P^2 , and parts of left P_2 , P_3^3 , P_4 and M_1
- SAM-PQ-L31278—right hemimandible, partly restored, with P_2 to M_1 (Fig. 6)
- SAM-PQ-L50304 and others—isolated cheek teeth (Figs 7, 8)
- SAM-PQ-L40969—left humerus (Fig. 9)
- SAM-PQ-L31957—right ulna lacking distal end (Fig. 10)
- SAM-PQ-L40846—right radius (Fig. 11)
- SAM-PQ-L30236, L31369—incomplete left innominates (Fig. 12)
- SAM-PQ-L30118, L45519—right femora (Fig. 13)
- SAM-PQ-L30424—left tibia and fibula, with latter lacking distal epiphysis (Fig. 14)

Diagnosis

As for genus.

Locality and horizon

The Varswater Formation, 'E' Quarry, Langebaanweg, Cape Province. The material described by Hendey & Repenning (1972) and L40846 and L40969 are from bed 3aS of the Pelletal Phosphorite Member, whilst most additional material, including others listed above, are from bed 3aN of the same member. Some material is also known from the Gravel and Quartzose Sand Members. (References: Hendey 1976; Dingle *et al.* 1979; Hendey 1980.)

Age

Langebaanian (latest Miocene/early Pliocene), between 3.5 and 7 Ma. (References: Hendey 1974, 1976, 1978a.)

Description

The descriptions which follow are confined to a few selected specimens, mostly collected since 1975, and are intended to supplement the descriptions in Hendey & Repenning (1972). Most of the material is from bed 3aN of the Pelletal Phosphorite Member and is, therefore, somewhat younger than that previously described, which is from bed 3aS. As with some other species common to these two horizons, there are minor morphological and possibly size differences between bed 3aS and bed 3aN representatives (Hendey 1978b, 1980). They are, however, too slight to warrant formal nomenclatural recognition, and simply reflect temporal stages of single species. This matter, as well as a detailed account of all the *Homiphoca capensis* material now available, will be the subjects of future studies.

The skull

Except where otherwise stated the following description is based on the paratype, L31976. This specimen is essentially similar in all observable respects to others from bed 3aN.



Fig. 3. Ventral view of *Homiophoca capensis* skull, SAM-PQ-L31976 (paratype).

The skull of *Homiphoca* is distinct from those of all living Phocidae, although it is unmistakably monachine and exhibits a combination of characters found in Monachini (*Monachus*) and Lobodontini (*Lobodon*, *Hydrurga*, *Leptonychotes*, *Ommatophoca*). Superficially it resembles the skulls of *Monachus* and *Lobodon* more than any other monachines.

There are prominent anterior tuberosities on the premaxillae, and in lateral view the anterior alveolar margin of the premaxillae recedes sharply posteroventrally from the apices of the tuberosities towards the crowns of the incisors and canines. The crowns of these teeth are themselves directed posteroventrally. A similar situation was observed during this study amongst living monachines only in *M. schauinslandi*, although it is much less obvious in this species. In addition, the premaxillary tuberosities of *M. schauinslandi* are more widely separated than in *Homiphoca*.

The premaxilla/maxilla suture is visible along its entire length in lateral view, as in phocines, but unlike the monachines, excluding *M. tropicalis*, in which the central part of the premaxillary ascending ramus is within the nasal aperture. In the phocines the laterally visible part of the ascending ramus is of constant width, but in *Homiphoca* that part in contact with the nasals is antero-posteriorly elongated. The phocine condition is similar to that in all other carnivores and is apparently the primitive one. Contact between the premaxillae and nasals is characteristic of *Monachus* but not Lobodontini.

Homiphoca has two pairs of upper incisors, which is typical of monachines, but these teeth are small compared with those of living species. They consist of a principal cusp anteriorly, with an inflated posterior cingulum which is almost in the form of an accessory cusp. The situation is similar in *M. monachus*, but not in *M. schauinslandi* and living Lobodontini. The lateral incisors are slightly larger than the medial ones, but the relative size difference is less than in other monachines, especially the Lobodontini, in which the lateral incisors (and canines) are enlarged, a specialization for opening breathing holes in sea ice. The *Homiphoca* incisors are likely to represent the primitive condition in monachines.

The roots (and alveoli) of the lateral incisors are oval-shaped in horizontal cross-section as in living Lobodontini, and unlike those of *Monachus*, which are circular. In L31976 the incisors are in a straight line, as in *M. tropicalis* and *M. schauinslandi*, but in other specimens, including the holotype, the incisor row curves posteriorly, although not as markedly as in *M. monachus* and the Lobodontini. In *Lobodon*, *Leptonychotes* and *Ommatophoca* the curvature is less obvious because of the procumbence of the lateral incisors.

The nasal bones of *Homiphoca* are elongated as in *M. tropicalis* and *M. schauinslandi*, and, judging from L30568 and L32101, are parallel-sided anteriorly and sharply tapering posteriorly, terminating above the orbits. The shape of the nasals in monachines is very variable, but of the Lobodontini those of *Hydrurga* are perhaps most like *Homiphoca*, except that the tapering commences further anteriorly. In *Homiphoca* the nasals are relatively wide



Fig. 4. Lateral view of *Homiphoca capensis* hemimandible, SAM-PQ-L31976 (paratype).

anteriorly, this being related to the overall width of the snout in this genus (see below). They are V-shaped anteriorly as in *M. tropicalis*, and the ethmoid (osseous nasal septum) is exposed between the branches of the V, unlike the situation in other monachines.

The ethmoid is a remarkably stout bone, and resembles those in *M. tropicalis*, *M. schauinslandi* and the Lobodontini, although that of *Lobodon* is distinct in being recessed within the nasal cavity. In *Homiphoca* the ethmoid extends to the posterior end of the nasal cavity. Viewed anteriorly the nasal aperture of *Homiphoca* is slightly dorsoventrally elongated, and in this respect is intermediate between *Monachus*, in which the aperture is circular or wider than it is high, and the Lobodontini, in which it is much higher than it is wide.

In *Monachus* the rostral region is more or less parallel-sided, but in *Homiphoca* it is broader posteriorly. The anterior tapering is very marked and the anterior part of the skull from the premaxillary tuberosities to the posterior extremity of the jugals is almost V-shaped in dorsal view. In this respect it differs from all living monachines. This distinctive shape is due largely to inflation of the maxillae posterolaterally above the three most posterior pairs of cheek teeth in L31976 and other bed 3aN specimens. This characteristic has not been observed in living monachines, nor is it found in the *H. capensis* holotype. It is evidently due to a greater development of the maxilloturbinals in the bed 3aN population of *Homiphoca*. The Lobodontini are also characterized by well-developed maxilloturbinals, but these are accommodated within the dorsoventrally expanded nasal cavity, without obvious deformation of the maxillae externally. The Phocinae also have well-developed maxilloturbinals and some have a posterolateral expansion of the maxillae similar to the bed 3aN

Homiphoca. The possible implications of this development in *H. capensis* will be discussed later (see p. 123).

The ascending branch of the *Homiphoca* maxilla is high and wide, having a lengthy contact with the nasals. Its anterior margin does not recede posteriorly as markedly as in other monachines, especially *Lobodon*. It is, however, more or less vertical and relatively high as in Lobodontini. By contrast, in *Monachus* the ascending branch is low and, viewed anteriorly, is strongly recurved medially, while in lateral view the snout is flattened anteriorly. These differences are reflected in the shape of the nasal apertures, and are due to the greater development of the turbinals in Lobodontini.

The pre-orbital process is relatively as prominent as that of *Hydrurga*. In other monachines it is small or absent. The infraorbital foramen is oval-shaped

TABLE 1
Dimensions of *Homiphoca capensis* paratype, SAM-PQ-L31976.

Overall length	270,0
Zygomatic width	165,0
Mastoid width	136,0
Width at supra-orbital processes	101,0
Minimum interorbital width	44,0
Width of premaxillae anteriorly	33,0
Length of nasals	69,5
Maximum width of nasals	25,0
Length of incisor row	23,5
Length of cheek tooth row	73,0
Width of palate between P ¹ 's	22,8
Width of palate between P ² 's	35,3
Width of palate between M ¹ 's	65,7
Overall length of mandible	185,0
Height of ascending ramus of mandible	71,0

	Length	Breadth	Lingual crown height
Lateral I	5,7	4,4	6,4
Medial I	4,7	3,4	4,8
<u>C</u>	9,1	4,4	8,2
P ¹	8,9	5,9	6,6
P ²	12,7	6,8	7,0
P ³	12,5	6,5	6,6
P ⁴	—	6,5	7,2
M ¹	8,6	5,5	7,7



Fig. 5. Dorsal, lateral and ventral views of *Homiphoca capensis* skull, SAM-PQ-L32101.

as in *Lobodon* and *Hydrurga*, but whereas in these genera the long axis is directed dorsomedially, in *Homiphoca* it is directed dorsolaterally (Hendey & Reppening 1972).

In L31976, and other bed 3aN specimens, the palate is concave anteriorly, but becomes convex on either side of the midline posteriorly. This is also due to expansion of the maxilloturbinal region of the nasal cavity. Unfortunately the posterior part of the palate in the *H. capensis* holotype is lost and it is not known if it lacked the expansion of this region, as it does the posterolateral expansion of the maxilla. In all other monachines the palate is either concave or more or less flat along its entire length. The same apparently applies in the case of phocines.

The dental arch of *Homiphoca* is not straight-sided as in Lobodontini, but diverges posteriorly from the P²'s, making the tooth-rows concave laterally as in *M. tropicalis*, and, less so, in *M. monachus* and *M. schauinslandi*. *Homiphoca* is like *Leptonychotes* in having a distinct diastema between P⁴ and M¹, but in *Homiphoca* the gap between these teeth is largely filled by M₁ when the jaws are closed, whereas in *Leptonychotes* the small M₁ comes into contact only with P⁴. The diastema between C and P¹ is variably developed in *Homiphoca*. For example, a small diastema is present in L31976 and L32101, but it is absent in the holotype, L30080 and L30568.

The C of *Homiphoca* is a relatively small and low-crowned tooth, which is circular in cross-section and with the crown recurved. Except perhaps for the recurvature it probably represents the primitive condition in monachines.

In terms of their basic morphology the upper premolars of *Homiphoca* are similar to their homologues in *Monachus*, and are very different from the specialized teeth of Lobodontini. They are, however, more slender than the premolars of *Monachus*. In addition, the P² to P⁴ are expanded posterolingually and thus taper anteriorly, whereas in *Monachus* the lingual margin is more or less semicircular in occlusal view. The P¹ is *Monachus*-like, but as with the other premolars it is lower crowned. The premolars have a prominent principal cusp, and accessory cusps anteriorly and posteriorly, with P² to P⁴ usually having a second, cingular cusp posteriorly. There is no cingulum buccally, but a well-developed one lingually. There is sometimes a small tubercle on the expanded posterolingual part of the cingulum (Fig. 7B). In this respect *Homiphoca* resembles *Lobodon* and *Hydrurga*, which may also have a small accessory cusp in the same position. It is not known in other monachines.

The premolars tend to wear horizontal facets on the principal cusps, which are later obliterated by sloping facets anteriorly. A similar sloping facet is sometimes present posteriorly. The wear on the premolars, especially P² to P⁴, indicates that these teeth had a crushing function like those of *Monachus*, but unlike those of Lobodontini. The premolars of *Homiphoca* and *Monachus* evidently represent the primitive and unspecialized condition in monachines. There are two reasons for believing that these teeth are 'primitive'. Their crushing function suggests that molluscs and crustaceans formed part of the diet,



Fig. 6. Lateral view of *Homiphoca capensis* hemimandible, SAM-PQ-L31278.

and such prey requires a lesser swimming ability on the part of predators than fast-swimming fishes and planktonic invertebrates. Greater swimming ability is obviously an advanced characteristic in phocids. Secondly, molluscs and larger crustacea occur in the littoral environment, the likely habitat of primitive phocids which had not yet adapted to a more pelagic way of life.

The M^1 of *Homiphoca* is distinguished from the premolars by having a strongly recurved and sharp-pointed principal cusp, and in having accessory cusps reduced or absent. A small accessory cusp is sometimes developed anteriorly. This tooth is ovate in occlusal view.

As in other monachines the palatines of *Homiphoca* become fused to the maxillae, and are well developed, reaching anteriorly to be in line with the M^1 's. The palatine foramen, through which the maxillary artery passes, is at the contact between the palatine and maxilla, whereas in all living monachines it is situated further anteriorly in the maxilla. In *Homiphoca* there is a groove for the maxillary artery passing anteriorly from the palatine foramen close to the lingual alveolar margin.

The intra-orbital part of the palatine is thick and the medial wall of the orbit is almost complete, as in *Hydrurga*. In other living Lobodontini this wall has large lacunae, which are reduced with age. This is apparently an advanced condition. The posterior border of the palatines, that is, the lower openings of the secondary choane, are oval in shape and resemble those in *Lobodon* and *Hydrurga*, rather than those of *Leptonychotes* and *Ommatophoca*.

The pterygoids of L31976 are poorly preserved, but it is evident that the pterygoid apophyses were small and that the lateral walls of the choane are nearly vertical as in *Hydrurga*.

The inter-orbital region is broad and tapers posteriorly, as in *Lobodon*, but in marked contrast to the condition in other monachines, notably *Monachus* and *Leptonychotes* in which the inter- and post-orbital regions are narrow and parallel-sided. The latter condition is apparently the primitive one.

As noted by Hendey & Repenning (1972), the jugal terminates anteriorly above the lateral border of the infra-orbital foramen in *Homiphoca*, above the centre of this foramen in *Monachus*, and lateral to this foramen in Lobodontini. *Homiphoca* is thus intermediate between the two groups of living monachines in this respect. The posterior end of the jugal is bifurcated, with a narrow dorsal branch and a broad ventral one, thus resembling *Monachus* in this respect, but differing from the Lobodontini.

The zygomatic process of the squamosal is short, with a pronounced dorsal inflection, while the glenoid fossa is narrow and deep. In both these respects *Homiphoca* is more like *Monachus* than Lobodontini.

The auditory region of the paratype is virtually identical to the one described in detail by Hendey & Repenning (1972). Other references to the ear region of *Homiphoca* are to be found in Ray (1976b) and Repenning & Ray (1977). A few additional observations are made here.

As noted by King (1966), the bulla covers the petrosal posteriorly in the

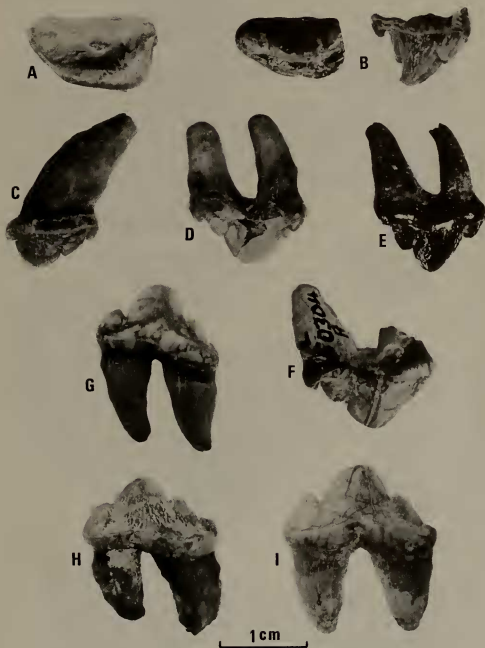


Fig. 7. *Homiphoca capensis* premolars. A. Occlusal view of upper left premolar, SAM-PQ-L55047B. B. Occlusal and anterior views of upper right premolar, SAM-PQ-L50304D. C. Lingual view of upper right premolar, SAM-PQ-L55046. D-F. Buccal views of upper right premolars, SAM-PQ-L55047C, 50304C, 50304A. G-I. Lingual views of lower right premolars, SAM-PQ-L55047A, L55047D, L50304B.

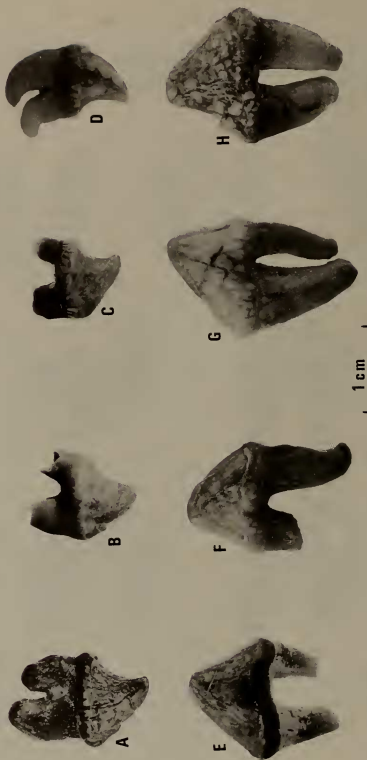


Fig. 8. *Homiophoca capensis* molars. A-D. Lingual views of right (A-C) and left (D) M_1 's. A. SAM-PQ-L50974. B. SAM-PQ-L55044B. C. SAM-PQ-L55044C. D. SAM-PQ-L55044A. E-H. Lingual views of right (E, G) and left (F, H) M_1 's. E. SAM-PQ-L55045D. F. SAM-PQ-L55045C. G. SAM-PQ-L55045B. H. SAM-PQ-L55045A.

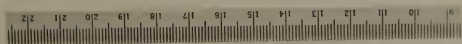


Fig. 9. Anterior, lateral and posterior views of *Homiphoca capensis* humerus, SAM-PQ-L-40969.

Lobodontini, whereas in *Monachus* the posterior part of the petrosal is exposed in ventral aspect. In *Homiphoca* the situation is intermediate, with the posterior extension of the bulla clearly less than in Lobodontini, and not covering the whole of the petrosal. In addition, the mastoid has a lip overlapping the posterior wall of the bulla. This condition is typical of the Lobodontini and its presence in *Homiphoca*, together with the posterior development of the bulla, is here regarded as good evidence of its relationship to this group (Hendey & Repenning 1972).

The bulla in *Homiphoca* is small and little inflated as in *Monachus*. The carotid foramen is located anteriorly as in *Lobodon* and *Ommatophoca*, but less so than in *Hydrurga* and *Leptonychotes*. The petrosal has been completely exposed in several *Homiphoca* specimens, showing that the promontorium is better developed than in *Monachus*, but less so than in Lobodontini. The apical whorls of the cochlea are visible and are not completely hidden by the considerably expanded basal whorls as in *Lobodon* and *Leptonychotes*. Once again the condition is intermediate between those in *Monachus* and Lobodontini (see Repenning & Ray 1977).

The basisphenoid is narrow as in *Hydrurga*, while the alisphenoid exhibits a well-developed lateral process as in *Monachus*. The basioccipital is relatively narrow and trapezoid in shape. In *Monachus*, *Lobodon*, and *Leptonychotes* the basioccipital is of similar shape but wider, while in *Hydrurga* and *Ommatophoca* it is narrow and sometimes rectangular.

In L31976, and some other *Homiphoca* specimens, there is a basioccipital foramen situated slightly posteriorly to, and medial of, the carotid foramen. On four of the specimens this foramen is situated at the basioccipital/bulla suture, while in two it is in the basioccipital itself. In spite of its variable position, it is apparently always present in *Homiphoca*, and may thus be characteristic of this taxon. It was otherwise observed in the present study only in three out of five *Hydrurga* skulls. In *Leptonychotes* there is a partially isolated basioccipital foramen at the anteromedial corner of the posterior lacerate foramen which may be homologous. The function of this foramen is not known. It may have accommodated a branch of the internal carotid artery, or, perhaps more likely, it may represent a branch of the ventral venous petrosal sinus. This foramen may be a primitive characteristic.

The exoccipitals carry triangular paroccipital processes which resemble those of *Monachus* and *Hydrurga*, but differ from the low crests observed in *Leptonychotes*. In *Lobodon* and *Ommatophoca* the crest is higher, but the process is not triangular.

The occipital condyles are similar to those of living monachines, while the foramen magnum is oval, which is commonly the case in living Lobodontini, whereas in *Monachus* it is usually circular.

The occipital crest is V-shaped as in *Lobodon*, *Leptonychotes* and *Monachus*, and not U-shaped as in *Hydrurga* and *Ommatophoca*. The braincase is relatively smaller than those of living Lobodontini, and similar to that of *Monachus*.



Fig. 10. Medial view of *Homiphoca capensis* ulna, SAM-PQ-L31957.



Fig. 11. Medial view of *Homiphoca capensis* radius, SAM-PQ-L40846.

Because the interorbital region is relatively broad, the anterior limit of the braincase is not as sharply defined as in *Monachus* and *Leptonychotes*. The anterior curvature of the braincase in dorsal view is gradual as in living Lobodontini. The sagittal crest is reduced as in *Lobodon* and *Leptonychotes*.

The *Homiphoca* skull is relatively narrow posteriorly, resembling those of *Lobodon* and *Hydrurga* more than other monachines in this respect (Fig. 15, Table 2).

The mandible of *Homiphoca* was previously described on the basis of a specimen lacking the teeth and those parts posterior to the cheek teeth, but largely complete specimens, many with one or more teeth in position, are now known. In general, the mandible is similar to that of *Monachus* and very different from those of the highly specialized Lobodontini.

The symphysis is short and terminates below the middle of P₂. In *Lobodon* and *Ommatophoca* it is much longer, reaching to below the anterior extremity of P₄, while in *Monachus*, *Hydrurga* and *Leptonychotes* it reaches to below the posterior extremity of P₂.

The horizontal ramus is low and narrow, and of constant height beneath the cheek teeth, much as in *Monachus*. The ascending ramus is also *Monachus*-like, with a very narrow coronoid process and large angular region, which gives it a rather square shape in lateral view. The condition in *Hydrurga* and *Ommatophoca* is similar, but these genera differ in having high condyles and much

TABLE 2
Mean dimensions and ratios of Lobodontini skulls.

	<i>Lobodon carcinophagus</i>	<i>Hydrurga leptonyx</i>	<i>Homiphoca capensis</i>	<i>Leptony- chotes weddelli</i>	<i>Ommato- phoca rossi</i>
N	11	6	3	10	4
1.	292	368	258	271	239
2.	98	116	87	65	47
3.	157	187	130	177	167
4.	87	105	72,5	86	81
2 : 1	0,335	0,315	0,337	0,239	0,196
4 : 3	0,554	0,561	0,557	0,485	0,485

N—Number of specimens (South African Museum collections).

1.—Overall length of skull.

2.—Length of snout from anterior extremity of premaxilla to anterior end of jugal.

3.—Height of occiput from basioccipital to top of occipital crest.

4.—Mastoid width.



Fig. 12. Lateral views of *Homiphoca capensis* innominates, SAM-PQ-L30236 and L31369.

smaller coronoid processes. The condyle is *Monachus*-like in being low and narrow, while the masseteric fossa is shallow and generally similar to that in *Monachus*.

Only three intact teeth remain in the paratype mandible, but other specimens have more complete dentitions, and hundreds of isolated teeth are available.

The lower incisors are small, nondescript teeth. The medial incisor is the smaller of the two, and is slightly more posteriorly situated. It lies almost horizontally in the mandible, whereas the lateral incisor is more vertically inclined. Both have a small posterior cingulum, as in *Monachus*. The \bar{C} is small, circular in cross-section and with a slightly recurved crown. The alveoli of the incisors and \bar{C} merge with one another at the alveolar margin.

The lower premolars are morphologically similar to the uppers, having a principal cusp, one anterior and two posterior accessory cusps. The lingual cingula are less pronounced than in *Monachus*, and in this respect *Homiphoca* is intermediate between *Monachus* and living Lobodontini. The lower premolars are narrower than the uppers and their homologues in *Monachus*. The postero-lingual cingula of P_2 to P_4 are slightly inflated.

The M_1 of *Homiphoca* is an unusual tooth, being unlike that of any previously recorded phocid. It has a large crown which is triangular in lateral view, and which is an elongated oval in occlusal view. The apex of the principal cusp is directed slightly posteriorly, with the result that the anterior keel is longer than the posterior one. Small anterior and posterior accessory cusps are sometimes present, the anterior one being the larger and situated slightly higher on the crown. A lingual cingulum, which may extend around the anterior end of the tooth, is present. It is similar to the M_1 of *Lobodon* in being larger than P_4 . In *Monachus* and in other Lobodontini the M_1 is smaller than P_4 . The *Homiphoca* M_1 is also unlike other double-rooted teeth of this taxon, and of living monachines, in having the roots converging towards their extremities.

The postcranial skeleton

Most elements of the postcranial skeleton of *Homiphoca capensis* are now available for study. Vertebrae, ribs, scapulae and innominates are generally incomplete, but most, if not all, limb bones are represented by several intact and well-preserved specimens. A vast number of incomplete limb bones are known.

Curiously, in view of the large number of additional *Homiphoca* specimens now available, the incomplete scapula described by Hendeby & Repenning (1972) is still one of the best specimens of this bone. A few supplementary observations are possible. The lower half of the posterior border of the blade of the scapula is triangular in cross-section as in *Monachus*, while in Lobodontini it is always rounded. The latter is an advanced condition which is discussed in more detail elsewhere (De Muizon 1979). The depression for the insertion of the triceps brachii on the posterolateral part of the neck is deep, indicating that this muscle was more powerfully developed than in living monachines



Fig. 13. Anterior and posterior views of *Homiphoca capensis* femora, SAM-PQ-L30118 and L45519.

The previously described humerii were incomplete, but several intact specimens are now known. In most living Lobodontini the greater trochanter is lower than the lesser trochanter. In some *Monachus* specimens they are of equal height, while in others the greater trochanter is higher, as in most carnivores. The latter is the primitive condition and is also found in late Miocene *Monotherium* of the North Atlantic and some of the phocids from the Pisco Formation in Peru (De Muizon 1979). In *Leptonychotes* and *Homiphoca* the development of the trochanters is intermediate between the primitive condition and the advanced one in other living Lobodontini.

Similarly, the lateral surface of the deltoid crest (from the greater trochanter to the deltoid tubercle) is more elongated in *Homiphoca* than in *Monachus*, and more like that in *Monotherium* and living Lobodontini. The prominent deltoid tubercle and strong relief of the posterolateral side of the deltoid crest indicate the existence of stronger brachialis and brachioradialis muscles in living Lobodontini than in Monachini.

The presence of a well-developed supinator ridge and entepicondylar foramen in the *Homiphoca* humerus is characteristic of phocines rather than monachines, and they are evidently primitive features. On the other hand, the deltoid/pectoral crest reaches the distal epiphysis in *Homiphoca*, and this is a typically monachine feature. The bicipital groove appears to be deeper and narrower than in most living monachines.

A comparison of the general morphology of the humerus of *Homiphoca* with those of *Monachus* and *Leptonychotes* suggests that it represents a primitive stage in the development towards the *Leptonychotes* (i.e. Lobodontini) condition. Particularly significant are the curvature in lateral view (it is straight in *Monachus*), size of the lesser trochanter and elongation of the muscle insertion area on the lateral side of the deltoid crest. In all these respects *Homiphoca* is closer to *Leptonychotes* than to *Monachus*.

The previously described ulnae represented the entire bone except for the tubercle for insertion of the anconeus medialis muscle. This tubercle is preserved in several new specimens, and, as in the Phocinae, it is very prominent. In this respect the ulna of *Homiphoca* differs from those of living monachines. The ulna of *Monotherium? wymani* (Ray 1976b) is similar to that of *Homiphoca*, and they evidently represent the primitive condition.

Complete radii are now known. The radius is very wide distally, as in *Monachus* and *Lobodon*. This represents a primitive condition relative to other Lobodontini, particularly *Leptonychotes* (De Muizon 1979). The *Homiphoca* radius differs from those of *Hydrurga* and *Ommatophoca* in that the area for insertion of the pronator teres is very pronounced in the latter genera.

No complete innominate bones are known, and the best available specimen is probably that described by Hendeby & Repenning (1972). This bone is typically monachine. The pectineal tuberosity was examined in ten specimens, and found to be reduced in seven, as in living Lobodontini, while in the others it is very prominent as in *Monachus* and the Phocinae. The psoas minor inserts on this



Fig. 14. Anterior and posterior views of *Homiphoca capensis* tibia and fibula, SAM-PQ-L30424.

tuberosity and it has the function of bending the back in the caterpillar-like terrestrial locomotion of seals. The stronger this muscle, the more terrestrial the species concerned is likely to be, and a prominent pectineal tuberosity may thus be interpreted as a primitive character. *Homiphoca* would thus have been more primitive than living Lobodontini in this respect, but more advanced than Monachini.

The femur of *Homiphoca* was previously described on the basis of a single distal fragment, but complete specimens are now known. This bone is short and wide as in living Lobodontini, but the head is more spherical and the neck is more distinct. In the latter respects it is *Monachus*-like. King (1966) recorded that the phocine femur was distinct from that of monachines in having a deep trochanteric fossa, a high trochanter and a pronounced popliteus pit. There are, however, exceptions amongst both monachines and phocines. For example, *Lobodon* has a deep trochanteric fossa, while in some Phocinae (e.g. *Erignathus*) it is absent. *Homiphoca* also has a trochanteric fossa, and, in addition, a well-developed popliteus pit. The trochanter is variably developed, sometimes being higher than the head as in the Phocinae, and sometimes lower as in the Lobodontini and *M. schauinslandi*. *Homiphoca* is probably most like *M. monachus* in this respect. In the Peruvian fossil monachines the trochanter is higher than the head and the popliteus pit is marked.

The anterior surface of the *Homiphoca* femur shaft has a marked concavity mediodistally. A similar concavity is often present in Lobodontini, but it is less pronounced in *Monachus*. The patella facet is transversely elongated as in Lobodontini. In the phocines this facet is dorsoventrally elongated. The area of insertion of the peroneus longus on the lateral epicondyle is very pronounced and visible in anterior view as in other Monachinae, whereas in Phocinae (excluding *Erignathus*) it is orientated laterally.

Although the phocid femur is more variable and less diagnostic than, for example, the humerus, the typically monachine *Homiphoca* femur is in some respects intermediate between those of *Monachus* and living Lobodontini. Of the latter it is perhaps closest to *Lobodon* because both have a deep trochanteric fossa.

The tibia and fibula of *Homiphoca* are fused proximally as in almost all living and fossil phocids. These bones are known to be articulated proximally only in *M. schauinslandi* (Ray 1976a) and a small monachine from the Pisco Formation in Peru.

The proximal tibial facets are usually markedly concave in the Phocinae and the tibial spine is high, while in living Monachinae the facets tend to be flat and the spine is low. The *Homiphoca* tibia is intermediate in these respects.

One of the most striking features of the *Homiphoca* tibia is the presence of very deep tibial fossae (Hendey & Repenning 1972). The posterior one extends along the proximal two-thirds of the shaft, and the anterior one along the proximal half of the shaft. A deep posterior fossa in seal tibiae indicates strong leg musculature. The *Homiphoca* tibia differs from those of living Lobodontini in

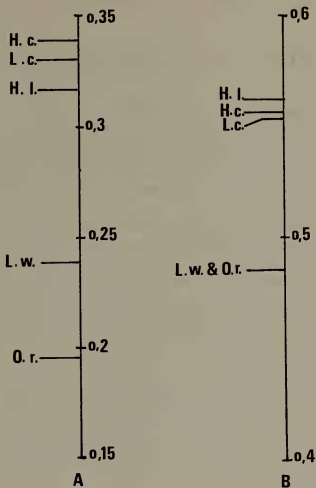


Fig. 15. Ratios of Lobodontini skull dimensions. A. Snout length: overall length. B. Occiput height: mastoid width. Data from Table 2. (H.c.—*Homiphoca capensis*, L.c.—*Lobodon carcinophagus*, H.l.—*Hydrurga leptonyx*, L.w.—*Leptonychotes weddelli*, O.r.—*Ommatophoca rossi*.)

being relatively short, and in terms of femur-tibia/fibula length proportions, *Homiphoca* is closer to *Monachus*. Possibly the more powerful musculature inserted on the tibia compensated for its relative shortness.

The anteroposteriorly flattened distal end of the tibia is similar to that of *Pliophoca* of the Italian Pliocene (Ugolini 1902; Tavani 1942).

The sharply angled distal fibula facet of the tibia led Hendey & Repenning (1972) to suggest that the fibula, which was then not known, must have been markedly bowed. In fact, the fibula is no more bowed than that of *Monachus*, although it is more so than in Lobodontini, in which the fibula is almost straight. The *Homiphoca* fibula has a small lateral recurved extension to the astragalus facet which articulates with the calcaneum. This facet is pronounced

in the Lobodontini and *Mirounga*, but is very reduced in *Monachus* and the Phocinae.

Most, if not all, elements of the *Homiphoca* manus and pes are now represented by complete specimens, but they are not described here.

DISCUSSION

It is abundantly clear that *Homiphoca capensis* is a member of the subfamily Monachinae, and in many respects is a morphological intermediate between living Monachini (*Monachus*) and Lobodontini (Hendey & Repenning 1972). *Monachus* is widely recognized as the least specialized of living Monachinae, while the Lobodontini are amongst the most highly specialized of all phocids. Hendey & Repenning (1972: 95) have already suggested that *H. capensis* is more specialized than *Monachus* and that in a 'broad sense' its relationships lie with 'the Antarctic monachines' (i.e. Lobodontini), although 'it is not clearly ancestral to any of the four living genera'. Subsequently it was suggested that *H. capensis* is more closely related to *Leptonychotes* and *Ommatophoca* than to *Lobodon* and *Hydrurga*, although it was probably not directly ancestral to either of the former (Hendey 1972). The present study has led to a revision of this opinion.

The informal separation of the Lobodontini into two groups, namely, *Leptonychotes* and *Ommatophoca* on the one hand, and *Lobodon* and *Hydrurga* on the other, is based in part on the following characters:

1. The highly specialized cheek teeth with well-developed accessory cusps of *Lobodon* and *Hydrurga* contrast with the reduced teeth of *Leptonychotes* and *Ommatophoca*, in which accessory cusps are absent in the former, and very small or absent in *Ommatophoca*.
2. The general development in *Lobodon* and *Hydrurga* of posterolingual cusps on the upper cheek teeth, which are absent in all other living monachines.
3. The molars (M_1^1) are well developed in *Lobodon* and *Hydrurga*, but are reduced in *Leptonychotes* and *Ommatophoca*.
4. The long snout in *Lobodon* and *Hydrurga* contrasts with the shortened one in *Leptonychotes* and *Ommatophoca* (Fig. 15).
5. The relatively high occiput in *Lobodon* and *Hydrurga* contrasts with the low occiput in *Leptonychotes* and *Ommatophoca* (Fig. 15).

The earlier opinion that *Homiphoca* was more closely related to *Leptonychotes/Ommatophoca* was based on the belief that while it would be possible for the teeth of the latter to evolve from those of *Homiphoca*, the M_1^1 of the latter was already more advanced than those of *Lobodon* and *Hydrurga*. The present study has suggested that this was not necessarily the case. In addition, there is other evidence which indicates that the relationships of *Homiphoca* lie rather with the *Lobodon/Hydrurga* group.

The most significant characteristics which *Homiphoca* shares with *Lobodon/Hydrurga* are as follows:

1. The posterolingual expansion of P^2 to P^4 , sometimes with a small accessory cusp.
2. The well-developed M_1 .
3. The relatively long snout (Fig. 15).
4. The relatively high occiput (Fig. 15).

At first sight the fact that the *Homiphoca* M^1 is relatively smaller than those of *Lobodon* and *Hydrurga* suggests that the former is unlikely to be closely related to either of these Antarctic genera. It is obvious that the M^1 of the most primitive Phocidae must have been large, and that the general trend in phocid evolution has been towards reduction of this tooth. Amongst living monachines it is only in *Lobodon* and *Hydrurga* that M^1 is similar in size, or only slightly smaller than P^4 .

All the teeth of *Lobodon* and *Hydrurga* are larger and more highly specialized than those of *Monachus*, which, except for their breadth, may well represent something approaching the condition typical of late Tertiary monachines. Since the M^1 of *Monachus* is relatively small, it is possible that the large size of this tooth in *Lobodon* and *Hydrurga* is a secondary development accompanying the general specialization of their dentitions. In other words, the large size of M^1 in these genera may be a specialized rather than primitive condition.

Another factor which suggests that the enlargement of the M^1 in *Lobodon* and *Hydrurga* was secondary is the parallel enlargement of P^1 in these genera. Both these teeth thus reflect a development towards homodonty, a condition which is characteristic of many marine mammals.

If the relatively large size of M^1 in *Lobodon* and *Hydrurga* is indeed a secondary specialization, then the size of this tooth in *Homiphoca* does not necessarily exclude it from being closely related to *Lobodon*/*Hydrurga*.

It may also be significant that the crown of the *Homiphoca* M_1 is, as in *Lobodon*, relatively higher than in any other known monachines. The fact that the *Homiphoca* M_1 was already enlarged relative to those of monachines other than *Lobodon* and *Hydrurga* may foreshadow the enlargement of M^1 in its descendants. The M^1 of *Lobodon* and *Hydrurga* is the least functional tooth in the dentitions in the sense that it alone is in contact with only one other tooth (M_1). For this reason its enlargement may have lagged behind that of M_1 and P^1_1 in the *Lobodon* and *Hydrurga* lineages.

The most striking aspect of the cheek teeth of *Lobodon* and *Hydrurga* is their highly specialized, comb-like cusps. It is therefore of interest to consider the manner in which monachine cheek tooth cusps might have evolved.

It was stated earlier that the cheek teeth of *Monachus*, a genus which is in almost all respects the least specialized of living monachines, are likely to resemble those of primitive members of the group. *Monachus* cheek teeth are comprised of a principal cusp, and, depending on species and tooth concerned, either no accessory cusps, one small posterior accessory cusp, or one small accessory cusp anteriorly and posteriorly. In those genera which are supposedly close to the origins of the Phocidae, such as *Paragale* and *Potamotherium*

(Savage 1957; Tedford 1976), the premolars (excluding P^4) have a principal cusp and reduced or absent accessory cusps, with never more than one of the latter anteriorly and posteriorly. It is, therefore, possible that primitive monachines were characterized by reduced or absent accessory cusps on their cheek teeth. It is worth noting in this connection that in the Otariidae accessory cusps are interpreted as an advanced character (Repenning & Tedford 1977: 66).

Late in the Tertiary there appears to have been a general tendency amongst phocids to develop accessory cusps, at least on the premolars, especially P_2^2 to P_4^4 . Subsequently, amongst the monachines different lineages evolved their cheek teeth in different ways. In *Monachus* there was probably little change in the teeth, just as the rest of the skull and postcranial skeleton remained unspecialized. In the *Leptonychotes*, *Ommatophoca*, and *Mirounga* lineages the cheek teeth were reduced and the accessory cusps were often lost. In the case of *Ommatophoca* it is known that during the early Pleistocene there was still the basic three-cusped pattern on P_2 to P_4 at least (King 1973). The *Lobodon* and *Hydrurga* lineages retained, and in the case of the former, even supplemented the three-cusped pattern on P_2^2 to P_4^4 , with individual cusps greatly enlarged and morphologically modified, while P_1^1 and M_1^1 evolved to match the characteristics of P_2^2 to P_4^4 .

In *Homiphoca* the cusp number on individual teeth is variable, but the situation may be summed up as follows:

1. P_1^1 have a well-developed posterior accessory cusp, and sometimes a small anterior and a second posterior accessory cusp as well. (Fig. 7C)
2. P_2^2 to P_4^4 have well-developed anterior and posterior accessory cusps, and sometimes a second small posterior accessory cusp. (Figs 7D-I)
3. M_1^1 sometimes has a posterior accessory cusp, and less often an anterior accessory cusp. (Figs 8E-H)
4. M^2 sometimes has a small anterior accessory cusp. (Figs 8A-D)

In addition, a small posterolingual cusp on P^2 to P^4 may be present (Fig. 7B).

Since *Homiphoca* cheek teeth have better developed, and sometimes also a greater number of accessory cusps than *Monachus*, it is possible that it belongs in that group of Lobodontini in which cheek tooth cusps are enlarged and well developed, that is, *Lobodon*/*Hydrurga*. The fact that it sometimes had one more cusp than *Hydrurga*, that is, the second posterior accessory cusp on P_2^2 to P_4^4 , which is the same in some *Lobodon* individuals, suggests that its affinities lie rather with the latter. However, *Lobodon* often has a third posterior accessory cusp on P_2^2 to P_4^4 , as well as one or two more cusps on its molars than *Homiphoca*. Presumably if *Homiphoca* did belong to a lineage in which cusps were being developed, it could have achieved the *Lobodon* condition in the lengthy time available.

There are other aspects of the accessory cusps in *Homiphoca* cheek teeth which suggest a possible connection with *Lobodon*. In the latter, those accessory cusps immediately adjacent to the principal cusp have their apices only a little below the level of the apices of the principal cusps. The homologous cusps in *Homiphoca* may also be relatively high on the keels of the principal cusps,

although they are never separated from the principal cusps as in *Lobodon*. This variation in position is particularly noticeable on M_1^1 , in which the anterior accessory cusps, when present, vary from being low on the anterior keel, at or near the cingulum, to a little way above it (Fig. 8). The significance of this is that when an accessory cusp is 'shifted' up the keel, it is then possible for an additional accessory cusp to develop from the cingulum anteriorly and posteriorly. It is apparently always from these positions that the supernumerary cusps of *Lobodon* cheek teeth are developed.

In addition, the supernumerary cingular cusps, like other accessory cusps in *Lobodon*, are curved in the direction of the principal cusp, a tendency which is apparent in *Homiphoca*. The best example of this in *Homiphoca* is in the isolated upper premolar, L50304A, in which there is a very pronounced anterior recurvature of the second posterior accessory cusp (Fig. 7F). This condition is not known in any other monachine.

Of course, the earlier alternative hypothesis that *Homiphoca* is more closely related to those Lobodontini in which teeth and accessory cusps are reduced or absent (i.e. *Leptonychotes/Ommatophoca*) cannot be dismissed. However, this alternative has no other compelling evidence to support it, whereas there are other characteristics which suggest a close relationship between *Homiphoca* and *Lobodon* (see p. 121). In addition, and perhaps most significantly, *Homiphoca* and *Lobodon* are similar in having a broad inter-orbital region, a characteristic which distinguishes them from other monachines.

In general the skulls of *Homiphoca* and *Lobodon* are similar in morphology and that of the former is only slightly smaller. The most striking differences are in the nasal region. In *Homiphoca* the nasals themselves are long, and the chambers occupied by the maxilloturbinals are voluminous, particularly in bed 3aN specimens in which there is deformation of the snout laterally and ventrally (see p. 101). In *Lobodon* the nasals are short, and the maxilloturbinals, although large and complex, are confined to the inter-orbital region. This contributes at least in part to the relatively broad post-orbital region of *Lobodon*.

The development of the maxilloturbinals is directly related to ambient air temperatures, since their mucosa serve to warm and moisten inspired air (Miller *et al.* 1964). The apparent differences in maxilloturbinal development between bed 3aS and bed 3aN *Homiphoca* populations may be related to the initiation of, or fluctuations within the major cooling of the late Tertiary. This cooling led to the cold upwelling within the Benguela Current System and consequent lowering of ambient air temperatures off the west coast of South Africa (see Siesser 1978).

It is thus likely that the maxilloturbinal development in bed 3aN *Homiphoca* was in an early stage of specialization. Refinement of the arrangement of the maxilloturbinals, perhaps by greater convolution, may have contributed to the marked difference in the nature of this region of the *Lobodon* skull.

The nasal cavity of *Lobodon* is also distinct in having two pronounced lateral fossae anterior to the maxilloturbinals. Their purpose is not known, but

they are presumably an advanced character related to nasal physiology. They have not been observed in other monachines, and they too contribute to the marked differences between the nasal regions of *Homiphoca* and *Lobodon*.

This, and other, differences between *Homiphoca* and *Lobodon* may all be interpreted as greater specialization in the latter, with adaptations being for different feeding habits, better aquatic locomotion, and life in a frigid climate. There appears to be no character which would preclude *Homiphoca* from being closely related to *Lobodon*. It does not necessarily follow that *Homiphoca* was directly ancestral to *Lobodon*, since it could equally have belonged on a separate lineage which paralleled that of *Lobodon* in some respects.

The origins of *Homiphoca* are obscure because of the extremely poor phocid record earlier in the Miocene. The best known of early phocids is *Monotherium*. Two late Miocene species are recorded in Belgium, namely, *M. aberratum* and *M. affine* (= *M. delognii*), while a middle Miocene species from North America is tentatively identified with this genus (*M. ? wymani*). The auditory region of the latter is known, and it has the mastoid lip overlapping the posterior wall of the bulla, a characteristic of *Lobodontini*. Although available evidence is slender, it is possible that *Monotherium* includes an ancestor of *Homiphoca*.

Other middle to late Miocene phocids are either not well enough known to be certain of their affinities, or obviously belong to groups other than the Lobodontini. *Prophoca rousseaui* from the middle Miocene of Belgium was referred by Ray (1976a) to the Phocinae, but its humerus appears to be typically monachine, and its relationships have yet to be firmly established by the discovery of additional material. *Callophoca* evidently is a monachine, but it is not relevant here since it is related to *Monachus* or *Mirounga* (Ray 1976a). The same applies to *Pliophoca*. The Paratethyan seals are very problematical, but they, too, are probably irrelevant to the history of the Lobodontini.

In conclusion some observations are made on the past distribution and dispersal of monachine seals.

It is almost certain that the Monachinae had their origins in the North Atlantic Ocean, and perhaps that the ancestors of *Homiphoca* reached the South Atlantic and South Africa by following the route suggested earlier by Hendeby (1972). This involved the dispersal of European monachines southwards along the north-west coast of Africa, across the north equatorial region of the Atlantic, down the east coast of South America, and back across the Atlantic in southern mid-latitudes, with the oceanic crossings being facilitated by major current systems. The latter were probably particularly significant in the case of the southerly dispersal of seals in the South Atlantic. The west to east route from South America to South Africa by way of subantarctic islands, which follows the prevailing current system in southern mid-latitudes, was used first by monachines and later by otariids. The latter must have entered the South Atlantic from the Pacific round the southern tip of South America, since early in their history they were confined to the Pacific Ocean.

It is possible that South Atlantic monachines took the same route followed

later by otariids. The time when monachines first entered the Pacific is not known, but it could have been as much as 15 m.y. ago (Repenning & Ray 1977). The older monachines of the Pisco Formation in Peru may be of late Miocene age and are the earliest known Pacific representatives of their subfamily. They clearly represent taxa distinct from *Homiphoca*, and their age relative to the latter is not certain.

It is also possible that South Atlantic monachines migrated along a more direct route southwards, either along the east coasts of the Americas, or along the west coast of Africa. The direction of major current systems does not necessarily directly influence the movements of seals along coastlines, whereas they are of paramount importance in oceanic crossings.

Although the last-mentioned alternative is not favoured, it, and the others, will remain possibilities until more relevant material from the regions in question is collected and studied.

SUMMARY

The status of recorded late Tertiary seals of the South Atlantic Ocean is revised. *Prionodelphis rovereti* from the late Miocene/early Pliocene of Argentina was identified by Frenguelli (1922) on the basis of five teeth belonging to a cetacean and one, or possibly two, monachine seals (Phocidae, Monachinae). *P. rovereti* is regarded as a cetacean. *Prionodelphis capensis* Hendey & Repenning, 1972, from South Africa is assigned to a new genus, *Homiphoca*.

A nearly complete skull and mandible, designated as a paratype of the species *H. capensis*, and most of the more significant postcranial bones, are described. These indicate that the genus is morphologically intermediate between monk seals, *Monachus* (Monachinae, Monachini), and Antarctic seals (Monachinae, Lobodontini) excluding *Mirounga*. The structure of the auditory region suggests a closer relationship with the Lobodontini, which are here informally divided into two groups, namely, *Leptonychotes/Ommatophoca* and *Lobodon/Hydrurga*. There is evidence to suggest that the affinities of *Homiphoca* lie with the latter group, and that it is likely to be more closely related to *Lobodon* than any other living seal. *Homiphoca* may have been derived from the North Atlantic *Monotherium* (Monachinae, Lobodontini), but the poor fossil record of primitive monachines makes this uncertain.

The possible migration routes followed by early monachines are examined, and it is suggested that the South Atlantic monachines probably followed the route suggested earlier by Hendey (1972).

RÉSUMÉ

La position des Phoques du Tertiaire supérieur de l'Atlantique Sud est ici révisée. *Prionodelphis rovereti* du Miocène supérieur/Pliocène inférieur d'Argentine fut décrit par Frenguelli (1922) sur la base de cinq dents appartenant à un Cétacé et un ou deux Monachinés (Phocidae, Monachinae). *P. rovereti* est

considéré comme un Cétacé. *Prionodelphis capensis*, HendeY et Repenning 1972, d'Afrique du Sud est assigné à un genre propre *Homiphoca* gen. nov.

Un crâne et une mandibule presque complets, désignés comme paratype de l'espèce *H. capensis*, et la plupart des éléments postcraniens les plus significatifs sont aussi décrits. Ce matériel montre que *H. capensis* est morphologiquement intermédiaire entre les Phoques moines *Monachus* (Monachinae, Monachini) et les Phoques antarctiques (Monachinae, Lobodontini) excluant *Mirounga*. La structure de la région auditive suggère un lien étroit avec les Lobodontini qui sont ici divisés en deux groupes, *Leptonychotes/Ommatophoca* d'une part et *Lobodon/Hydrurga* d'autre part. Plusieurs arguments suggèrent un rapprochement d'*Homiphoca* avec le second groupe et plus précisément avec le genre *Lobodon*. *Homiphoca* pourrait avoir son origine dans le genre *Monotherium* (Monachinae, Lobodontini) de l'Atlantique Nord mais cette hypothèse reste incertaine compte tenu de la pauvreté du matériel des Monachinae fossiles.

Les routes de migration possibles, suivies par les premiers Monachinés, sont envisagées et il est suggéré que les Monachinae de l'Atlantique Sud ont probablement utilisé la route proposée par HendeY (1972).

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REFERENCES

- AMEGHINO, F. 1886. Contribución al conocimiento de los mamíferos fósiles de los terrenos antiguos terciarios del Paraná. *Boln Acad. nac. Cienc. Córdoba* 9: 1-228.
- AMEGHINO, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. *Actas Acad. nac. Cienc. Córdoba* 6: 129-167.
- BUDACK, K. F. R. 1977. The \neq Aonin or Topnaar of the lower !Khuiseb valley and the sea. *Khoisan Linguistic Studies* 3: 1-41.
- BURMEISTER, G. 1885. Examen crítico de los mamíferos y reptiles fósiles denominados por D. Augusto Bravard y mencionados en su obra precedente. *An. Mus. nac. Buenos Aires* 3: 95-174.
- CABRERA, A. 1926. Cetáceos fósiles del Museo de la Plata. *Revta Mus. La Plata* 29: 363-411.
- DINGLE, R. V., LORD, A. R. & HENDEY, Q. B. 1979. New sections in the Varswater Formation (Neogene) of Langebaan Road, south-western Cape, South Africa. *Ann. S. Afr. Mus.* 78: 81-92.

- EICHWALD, C. E. 1853. *Lethaea Rossica, ou Paleontologie de la Russie*. 3. Stuttgart: Schweizerbart.
- FRENGUELLI, J. 1922. *Prionodelphis rovereti* un representante de la familia 'Squalodontidae' en el Paranense Superior de Entre Ríos. *Boln Acad. nac. Cienc. Córdoba* 25: 491-500.
- FRENGUELLI, J. 1926. El Entrerriense de Golfo Nuevo en el Chubut. *Boln Acad. nac. Cienc. Córdoba* 29: 191-270.
- GRIGORESCU, D. 1976. Paratethyan seals. *Syst. Zool.* 25: 407-419.
- HENDEY, Q. B. 1972. The evolution and dispersal of the Monachinae (Mammalia: Pinnipedia). *Ann. S. Afr. Mus.* 59: 99-113.
- HENDEY, Q. B. 1974. The late Cenozoic Carnivora of the south-western Cape Province. *Ann. S. Afr. Mus.* 63: 1-369.
- HENDEY, Q. B. 1976. The Pliocene fossil occurrences in 'E' Quarry, Langebaanweg, South Africa. *Ann. S. Afr. Mus.* 69: 215-247.
- HENDEY, Q. B. 1978a. Late Tertiary Hyaenidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. *Ann. S. Afr. Mus.* 76: 265-297.
- HENDEY, Q. B. 1978b. Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Ann. S. Afr. Mus.* 76: 329-357.
- HENDEY, Q. B. 1980. *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Ann. S. Afr. Mus.* 81: 1-109.
- HENDEY, Q. B. & REPENNING, C. A. 1972. A Pliocene phocid from South Africa. *Ann. S. Afr. Mus.* 59: 71-98.
- KELLOGG, R. 1942. Tertiary, Quaternary and Recent marine mammals of South America and the West Indies. *Proc. 8th Am. Sci. Congr. (Washington)* 3: 445-473.
- KING, J. E. 1956. The monk seals (genus *Monachus*). *Bull. B. Mus. nat. Hist. (Zool.)* 3: 201-256.
- KING, J. E. 1964. *Seals of the world*. London: British Museum (Natural History).
- KING, J. E. 1966. Relationships of the hooded and elephant seals (genera *Cystophora* and *Mirounga*). *J. Zool.* 148: 385-398.
- KING, J. E. 1973. Pleistocene Ross seal (*Ommatophoca rossi*) from New Zealand. *N. Z. J. Marine Freshwater Res.* 7: 391-397.
- KRAGLIEVICH, L. 1934. La antigüedad pliocena de las faunas de Monte Hermosa y Chapadmalal. *Siglo Ilustrado, Montevideo* 938: 1-136.
- MARSHALL, L. 1978. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *Univ. Calif. Publ. geol. Sc.* 117: 1-89.
- MILLER, M. E., CHRISTENSEN, G. C. & EVANS, H. E. 1964. *Anatomy of the dog*. Philadelphia: W. B. Saunders.
- MUIZON, C. DE 1979. Contribution à l'étude systématique, anatomique et fonctionnelle des Phocidae Pliocènes de la Formation Pisco (Pérou). Considérations générales sur la phylogénie et la paléobiogéographie des Phocidae. Unpublished thesis, Université Pierre et Marie Curie, Paris 6.
- RAY, C. E. 1976a. Geography of phocid evolution. *Syst. Zool.* 25: 391-406.
- RAY, C. E. 1976b. *Phoca wymani* and other Tertiary seals (Mammalia: Phocidae) described from the eastern seaboard of North America. *Smithsonian Contr. Paleobiol.* 28: 1-36.
- RAY, C. E. In press. Seals and walruses (Mammalia: Pinnipedia) of the Yorktown Formation of Virginia and North Carolina. *Smithsonian Contr. Paleobiol.*
- REPENNING, C. A. & RAY, C. E. 1977. The origin of the Hawaiian monk seal. *Proc. Biol. Soc. Washington* 89: 667-688.
- REPENNING, C. A. & TEDFORD, R. H. 1977. Otarioid seals of the Neogene. *U.S. geol. Surv. Prof. Paper* 992: 1-93.
- SAVAGE, R. J. G. 1957. The anatomy of *Potamotherium*, an Oligocene lutrine. *Proc. zool. Soc. Lond.* 129: 151-244.
- SCHIEFFER, V. B. 1958. *Seals, sea lions and walruses*. Stanford: University Press.
- SIESSER, W. G. 1978. Aridification of the Namib Desert: Evidence from oceanic cores. In: VAN ZINDEREN BAKKER, E. M. ed. *Antarctic glacial history and world palaeoenvironments*: 105-113. Rotterdam: Balkema.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. nat. Hist.* 85: 1-350.
- TAVANI, G. 1942. Revisione dei resti di pinnipedi conservato nel Museo di Geologia di Pisa. *Palaeontogr. ital.* 40: 97-113.

- TEDFORD, R. H. 1976. Relationships of pinnipeds to other carnivores (Mammalia). *Syst. Zool.* 25: 363-374.
- TROUSSERT, E. L. 1898. *Catalogus mammalium tam viventium quam fossilium*. Berlin: Friedlander.
- UGOLINI, R. 1902. Il *Monachus albiventer* Bodd. del Pliocene di Orciano. *Palaeontogr. ital.* 8: 1-20.
- VAN BENEDEN, P. J. 1877. Description des ossements fossiles des environs d'Anvers. *Ann. Mus. r. Hist. nat. Belg.* 1: 1-88.